

## Oxygen Consumption Rate and Swimming Efficiency of the Blacknose Shark, *Carcharhinus acronotus*

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Oxygen consumption rates and swimming efficiency of 10 blacknose sharks (47–87 cm total length and 0.45–3.51 kg weight), *Carcharhinus acronotus*, were determined using a closed, circular respirometer. Swimming speed ranged from 20–40 cm sec<sup>-1</sup> and averaged 30.8 (± 0.48 SE) cm sec<sup>-1</sup>. Routine weight specific oxygen consumption rates increased from 278.5 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> for a 3.5 kg shark to 486 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> for a 0.8 kg shark. The relationship of swimming speed and weight specific oxygen consumption rate for sharks 0.45–0.85 kg was described by the equation  $\log V_{O_2} = 0.007 U + 2.38$ ,  $r^2 = 0.31$ ,  $P = 0.006$ , where  $U$  is swimming speed in cm sec<sup>-1</sup>. Mean standard metabolic rate, the amount of oxygen consumed at zero activity, was calculated by extrapolating to zero swimming speed and was 239.8 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>. Total cost of transport (cal g<sup>-1</sup> km<sup>-1</sup>), the energy required to travel a given distance at a particular speed, was used as a measure of overall swim efficiency. Highest total cost of transport (1.68 cal g<sup>-1</sup> km<sup>-1</sup>) was at 25 cm sec<sup>-1</sup> and decreased with increasing speed. Swimming efficiency was optimal at speeds of 36–39 cm sec<sup>-1</sup>. Results suggest blacknose sharks have higher routine oxygen consumption rates and total cost of transport, but the cost of locomotion was similar to other active, tropical sharks.

**S**TUDIES on shark oxygen consumption rates are important for calculating swimming efficiency, for constructing energy budgets, and for overall bioenergetic analysis. Most studies have focused on relatively inactive, cooler water sharks such as spotted dogfish, *Scyliorhinus stellaris*, (Piiper and Schumann, 1967; Metcalf and Butler, 1984); spiny dogfish, *Squalus acanthias*, (Brett and Blackburn, 1977); leopard shark, *Triakis semifasciata*, (Scharold et al., 1989); and lesser spotted dogfish, *Scyliorhinus canicula* (Sims, 1996).

Some studies on the oxygen consumption rate of more active, tropical species have been conducted. Bushnell et al. (1989) studied the oxygen consumption rate of the lemon shark, *Negaprion brevirostris*, using an annular respirometer and Graham et al. (1990) studied the swimming performance of lemon shark under controlled swimming speeds using a water tunnel. However, many active, tropical shark species in the Order Carcharhiniformes are obligate ram-ventilators and must swim continuously to ventilate the gills and maintain hydrostatic equilibrium. Continuous swimming by these sharks could result in higher oxygen consumption rates. Lemon sharks, however, undergo periods of resting (Gruber, 1982; Bushnell et al., 1989), and estimations of oxygen consumption rate may be lower than would be expected for an obligate ram-ventilating species.

There are limited studies on the oxygen consumption rates of obligate ram-ventilating

sharks. Graham et al. (1990) reported the oxygen consumption rate of mako shark, *Isurus paucus*, approached that of tunas, whereas Parsons (1990) suggested the oxygen consumption rate of the bonnethead shark, *Sphyrna tiburo*, was similar to that of typical active bony teleosts. These results suggest that oxygen consumption rate among obligate ram-ventilating sharks is variable, and further work is necessary to verify oxygen consumption rate in this group of sharks.

Our objectives for this study were to report on the oxygen consumption rate and swimming efficiency of the blacknose shark, *Carcharhinus acronotus*. In addition to increasing the information on oxygen consumption rate of obligate ram-ventilating sharks, we wish to compare our results of oxygen consumption rate with those for other species of sharks to further quantify the swimming efficiency of obligate ram-ventilating shark species.

### MATERIALS AND METHODS

Blacknose sharks, 47–87 cm total length (TL) and 0.45–3.51 kg weight, were captured using gill nets, longlines, and rod and reel from the St. Andrew Bay System, Florida, and transported to the National Marine Fisheries Service Laboratory, Panama City, Florida. At the laboratory, sharks were held for up to three months in outdoor, shaded, circular 3000-liter tanks with a flow-through seawater system or in a 20 × 15 ×

1.5 m outdoor-fenced, natural lagoon adjacent to the laboratory. Sharks were fed to satiation every other day on a diet of squid or fish. Prior to experimentation, sharks were not fed for 96 h to achieve a postabsorptive state.

Swimming speed and oxygen consumption rate measurements ( $\text{VO}_2$ ) were made in a closed, circular, respirometer (inner diameter 182 cm  $\times$  depth 58 cm) constructed using a modified 1500-liter polyethylene tank. The tank was permanently sealed using silicon sealant and a plywood and plexiglas lid. Plexiglas windows cut into the sides and top of the respirometer allowed for observations during experiments. One window in the lid was removable, allowing for placement and removal of the shark from the respirometer.

The respirometer was filled with filtered, ultraviolet sterilized, seawater at  $30 (\pm 0.6 \text{ SD})$  ppt salinity and  $28 (\pm 0.9 \text{ SD})$  C. A shark was placed in the respirometer and allowed to acclimate for 24 h. A Microelectrodes polarographic oxygen electrode (Model MI-730) connected to a Microelectrodes amplifier (Model OM-3) and Linseis strip chart recorder (Model L-4000) was calibrated at the experimental temperature and pressure prior to insertion into the respirometer. The respirometry system was interfaced with a laptop computer equipped with the UNISOFT® program. During the experiment, sharks swam continuously around the outer edge of the respirometer which allowed for water mixing. Preceding and immediately after each experiment, oxygen concentration and temperature were verified using a YSI Model 51B oxygen meter. A blank respirometer was measured for 4 h to determine background respiration.

Swimming speed ( $\text{cm sec}^{-1}$ ) was measured every 15–30 min. Replicate measurements were determined by noting the time required for the shark to pass between two points of a known distance marked on the respirometer.

Oxygen consumption rate (corrected for background respiration) was calculated using the equation:

$$\text{VO}_2 = b \cdot v \cdot s$$

where  $\text{VO}_2$  is oxygen consumption rate in  $\text{mg O}_2 \text{ h}^{-1}$ ,  $b$  is the rate of change of oxygen in the respirometer,  $v$  is the volume of the respirometer (1500 liter), and  $s$  is the solubility of oxygen calculated at the experimental temperature and pressure. When dissolved oxygen concentrations reached  $5.0 \text{ mg l}^{-1}$ , the seal was broken on the tank, the shark was removed from the respirometer, weighed ( $\text{kg} \pm 0.01$ ), measured (total length,  $\text{cm} \pm 1.0$ ), and returned to the hold-

ing area. Experiments were conducted under constant light conditions to eliminate exogenous environmental cues. The water in the respirometer was replaced after each experiment. No sharks died as a result of these experiments, and all were later released.

Oxygen consumption rate (per unit body weight) for each shark was pooled into swimming speed intervals ( $\pm 1.0 \text{ cm sec}^{-1}$ ). Oxygen consumption rate for each interval was calculated, and a regression analysis was used to describe the relationship between swimming speed and  $\text{VO}_2$ . A swimming speed interval was determined as the speed maintained for a 1-h period. This was done to guarantee that  $\text{VO}_2$  recorded accurately reflected the specific swimming speed measured. Shark swimming speed was not controlled, but this was not problematic because sharks would maintain similar swimming speeds for long periods of time.

Oxygen consumption rate was converted to metabolic rate using the oxycaloric coefficient for fish of  $3.25 \text{ cal mg O}_2^{-1}$  (Brafield and Solomon, 1972). Total cost of transport ( $\text{cal g}^{-1} \text{ km}^{-1}$ ), the energy required to travel a given distance at a particular speed, was determined by dividing the metabolic rate ( $\text{cal g}^{-1} \text{ h}^{-1}$ ) by swimming speed ( $\text{km h}^{-1}$ ) and used to provide an estimate of overall swimming efficiency (Schmidt-Nielsen, 1972).

## RESULTS

Swimming speed, for 10 blacknose sharks, ranged from 20–40  $\text{cm sec}^{-1}$  and averaged 30.8  $\text{cm sec}^{-1}$ . The percent change in oxygen consumption fluctuated from 0.5–12%  $\text{h}^{-1}$  for all sharks. Oxygen consumption rate (per unit body weight) varied from a minimum of 202  $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$  to a maximum of 797  $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$  (Table 1). Routine oxygen consumption rate, determined as the grand mean of all  $\text{VO}_2$  measured regardless of swimming speed, ranged from 278.5  $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$  for a 3.5 kg shark to 486  $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$  for a 0.8 kg shark.

Blacknose shark oxygen consumption rate increased with swimming speed. By log transforming  $\text{VO}_2$  data, a linear regression equation described the relationship between swimming speed and  $\text{VO}_2$ . The relationship of swimming speed and  $\text{VO}_2$  for sharks 0.45–0.85 kg (mean weight =  $0.56 \pm 0.01 \text{ kg}$ ;  $n = 8$ ) was described by the equation  $\log \text{VO}_2 = 0.007 U + 2.38$ ,  $r^2 = 0.31$ ,  $P = 0.006$ , where  $\text{VO}_2$  = oxygen consumption rate in  $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$  and  $U$  is swimming speed in  $\text{cm sec}^{-1}$  (Fig. 1). Standard oxygen consumption rate, the amount of oxygen consumed at zero activity, was calculated by extrap-

TABLE 1. EXPERIMENTAL RUNS FOR BLACKNOSE SHARK SUMMARIZING TEMPERATURE, WEIGHT, TOTAL LENGTH, SWIMMING SPEED, AND OXYGEN CONSUMPTION RATE ( $\text{VO}_2$ ). Numbers are  $\pm$  standard error.

Shark No.	Temp. (C)	Weight (kg)	Total length (cm)	Swimming speed range (cm sec <sup>-1</sup> )	Mean swimming speed (cm sec <sup>-1</sup> )	Mean swimming speed (l sec <sup>-1</sup> )	$\text{VO}_2$ range (mg O <sub>2</sub> kg <sup>-1</sup> h <sup>-1</sup> )	Mean $\text{VO}_2$ (mg O <sub>2</sub> kg <sup>-1</sup> h <sup>-1</sup> )
1	27	0.75	57	29–35	31.0 $\pm$ 0.6	0.54 $\pm$ 0.01	202–760	400.0 $\pm$ 92.5
2	28	0.85	66	20–38	31.8 $\pm$ 0.7	0.48 $\pm$ 0.01	237–713	456.0 $\pm$ 34.7
3	28	0.47	46	20–38	31.3 $\pm$ 0.8	0.69 $\pm$ 0.02	265–797	464.9 $\pm$ 45.3
4	28	0.45	47	26–39	33.4 $\pm$ 1.1	0.71 $\pm$ 0.02	255–737	334.0 $\pm$ 84.8
5	28	0.81	63	29–38	33.6 $\pm$ 1.2	0.53 $\pm$ 0.02	262–648	486.0 $\pm$ 113.2
6	28	3.51	87	30–40	31.4 $\pm$ 2.0	0.36 $\pm$ 0.02	250–297	278.5 $\pm$ 20.3
7	27	1.56	71	30–38	32.1 $\pm$ 0.6	0.58 $\pm$ 0.01	288–576	384.0 $\pm$ 37.6
8	28	0.63	55	20–39	31.4 $\pm$ 1.4	0.61 $\pm$ 0.02	219–400	381.0 $\pm$ 11.6
9	29	0.55	51	27–36	30.0 $\pm$ 0.4	0.59 $\pm$ 0.01	205–514	377.0 $\pm$ 27.6
10	29	0.45	45	26–35	30.3 $\pm$ 0.6	0.67 $\pm$ 0.01	219–408	408.3 $\pm$ 23.2

olating to zero swimming speed (Brett, 1964) and was 239.8 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>. Oxygen consumption rate–swimming speed relationships for larger sharks (1.5 and 3.5 kg) were not constructed because of the limited range of swimming speeds exhibited by these sharks.

Total cost of transport (TCT) decreased with increasing speeds for blacknose sharks (Fig. 2). Highest TCT was 1.68 cal g<sup>-1</sup> km<sup>-1</sup> at 25 cm sec<sup>-1</sup> and decreased to lowest TCT of 0.9 cal g<sup>-1</sup> km<sup>-1</sup> at 39 cm sec<sup>-1</sup>.

#### DISCUSSION

Routine oxygen consumption rate estimates for blacknose sharks are among the highest yet measured for an active tropical shark but do not approach that of the mako shark when corrected for temperature differences (Table 2). The

lemon shark routine metabolic rate is 110 ml O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> at 22 C (Bushnell et al., 1989) and the bonnethead shark is 246 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> at 25 C (Parsons, 1990). Graham et al. (1990) determined an oxygen consumption rate of 318 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> for a single lemon shark under controlled speeds of 65–91 cm sec<sup>-1</sup> at an average temperature of 22.4 C. However, the variance in experimental temperature, size and swimming speed of the animal, discerning the differences between oxygen consumption rates (e.g., routine or active), and the variability in methods used to obtain them makes comparison among species difficult and should be interpreted with caution. Still, even after compensation for differences in experimental temperatures by applying a  $Q_{10}$  of 2.3 (Brett and Groves, 1979),

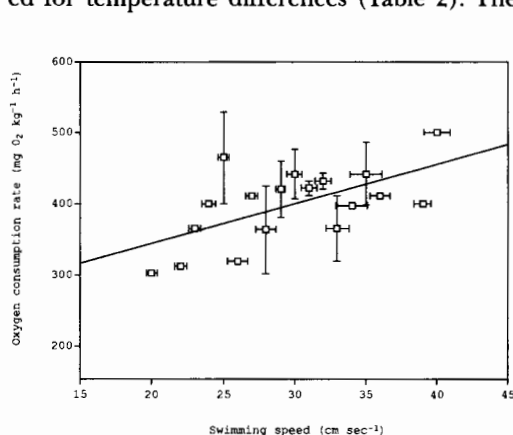


Fig. 1. Oxygen consumption rate (mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>) in relation to absolute swimming speed for blacknose shark. Each box represents the mean  $\text{VO}_2$  for the swimming speed interval determined for all sharks 0.45–0.85 kg (mean weight = 0.56 kg; n = 8). Vertical and horizontal lines are standard errors.

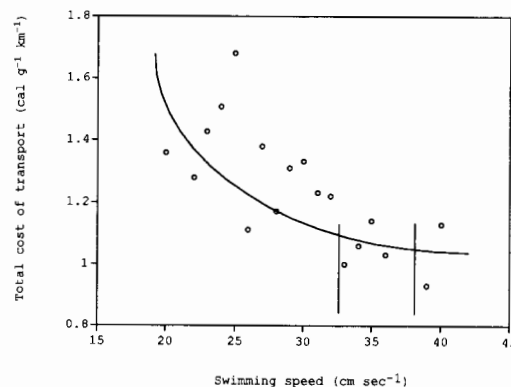


Fig. 2. Mean total cost of transport for blacknose sharks as a function of swimming speed. Each point represents the mean cost of transport for the swimming speed interval determined for all sharks 0.45–0.85 kg (mean weight = 0.56 kg; n = 8). Curve is fit-by-eye to data points. The range of predicted optimal swimming velocity (Weihs et al., 1981) for sharks 46–66 cm TL is indicated by the two vertical lines.

TABLE 2. SUMMARY OF THE OXYGEN CONSUMPTION RATES REPORTED IN THE LITERATURE FOR SHARK SPECIES CALCULATED AT THE EXPERIMENTAL TEMPERATURE AS WELL AS CORRECTED FOR A TEMPERATURE OF 28 °C BY APPLYING A  $Q_{10}$  OF 2.3 (BRETT AND GROVES, 1979). Swimming speed values reported in body length  $\text{sec}^{-1}$  were converted to  $\text{cm sec}^{-1}$  for comparison. Oxygen consumption rates denoted by (\*) are considered active rates; defined as the maximum rate of oxygen consumption at the maximum sustained speed (Brett and Groves, 1979).

Species	Weight (kg)	Temp. (°C)	Swimming speed ( $\text{cm sec}^{-1}$ )	$\text{VO}_2$ ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ )	$\text{VO}_2$ ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ ) @ 28 °C	Reference
<i>Carcharhinus acronotus</i>	1.0	28	32	395	395	present study
<i>Isurus oxyrinchus</i>	3.9	16–20	24.6	369	849	Graham et al. (1990)
<i>Negaprion brevirostris</i>	0.8–1.3	22	17–24	110	152	Bushnell et al. (1989)
<i>Negaprion brevirostris</i>	1.65	22–25	65–91	318	382	Graham et al. (1990)
<i>Sphyrna tiburo</i>	1.0	25	35	247	296	Parsons (1990)
<i>Squalus acanthias</i>	2.0	10	5	49	202	Brett and Blackburn (1978)
<i>Triakis semifasciata</i>	2.2–5.8	16.4	62	167*	384	Scharold et al. (1989)

blacknose shark routine oxygen consumption rate still exceeds that of lemon and bonnethead sharks.

The relationship between swimming speed and  $\text{VO}_2$  were similar among shark species. The slopes determined for blacknose sharks are similar to lemon shark (Bushnell et al., 1989), leopard shark (Scharold et al., 1989) and scalloped hammerhead, *Sphyrna lewini* (C. Lowe, pers. comm.). However, the intercept (standard  $\text{VO}_2$ ) was highest for ram-ventilating species like blacknose and scalloped hammerhead shark and lowest for leopard shark. The high standard  $\text{VO}_2$  found for ram-ventilating species could be due to a larger gill surface area for increased oxygen uptake, but the increased surface area requires more energy for osmoregulation (Stevens, 1972). Moreover, Brill (1996) suggested the high standard oxygen consumption rate found in tunas was also due to their large gill surface area and the increased energetic costs of osmoregulation.

The relationship of total cost of transport with swimming speed in blacknose sharks was generally similar to trends observed in other species (Brett, 1963; Parsons and Sylvester, 1992; Dewar and Graham, 1994). The trend is initially high, declines, goes through a set of minimum values defined as the optimal swimming speed, and then increases as  $\text{VO}_2$  rises with swimming speed as the power to overcome friction and form drag increases (Videler and Nøt, 1990). However, a significant increase in total cost of transport values beyond the optimal swimming speed was not observed in blacknose sharks likely because of the inability to induce sharks to swim at higher velocities.

The optimal swimming velocity is defined as

the velocity where energy expenditure per unit distance is minimized. Weihs (1977) developed a theoretical model of cost-optimization and obtained relatively accurate estimations of shark swimming speed (Weihs et al., 1981). Results from this study for blacknose sharks 46–66 cm TL suggest an optimal swimming velocity of about 36–39  $\text{cm sec}^{-1}$ , which is similar to the optimal swimming velocity of about 32–38  $\text{cm sec}^{-1}$  predicted by Weihs et al. (1981). Parsons and Sylvester (1992) also found optimal swimming velocities for white crappie, *Pomoxis annularis*, to correspond to predicted velocities of Weihs et al. (1981). However, it is still unclear whether free-ranging sharks swim at the predicted optimal velocity.

The total cost of transport provides a relative index of overall swimming efficiency. Using the oxygen consumption rate–swimming speed relationship for 0.8–1.3 kg lemon sharks (Bushnell et al., 1989) and correcting for temperature differences, TCT at 36–39  $\text{cm sec}^{-1}$  is 0.47–0.50  $\text{cal g}^{-1} \text{ km}^{-1}$ . Blacknose sharks at similar swimming speeds have a TCT of 0.90–1.03  $\text{cal g}^{-1} \text{ km}^{-1}$ . This indicates that, at similar swimming speeds, blacknose shark consume 52% more energy. However, examination of locomotor efficiency requires calculation of net cost of transport (the cost of transport calculated using the difference between standard and active metabolic rate). Net cost of transport at 36–39  $\text{cm sec}^{-1}$  for blacknose sharks ( $\sim 0.3 \text{ cal g}^{-1} \text{ km}^{-1}$ ) was similar to that calculated for lemon shark ( $\sim 0.4 \text{ cal g}^{-1} \text{ km}^{-1}$ ). The similarity in costs of locomotion between lemon and blacknose sharks are likely a result of their similar morphology which is designed for cruising (Thompson and Simanek, 1977).

This study suggests that blacknose shark routine oxygen consumption rate exceeds previously studied lemon and bonnethead sharks but does not approach that of the mako shark. Blacknose sharks have higher routine oxygen consumption rates, but the cost of locomotion was similar to that calculated for lemon sharks. The higher oxygen consumption rates found for blacknose sharks is likely a result of their higher standard rate and its influence on overall routine oxygen consumption rates. Optimal swimming speed was determined to be about 36–39 cm sec<sup>-1</sup> and corresponded well with the predicted optimal velocity of Weihs et al. (1981). However, the swimming model proposed in this study may not reflect the entire range of VO<sub>2</sub> because swimming speed was not controlled and blacknose shark may swim at much higher levels than found here. Future investigations should focus on measuring the maximum oxygen consumption rates of blacknose shark and additional obligate ram-ventilating shark species under controlled swimming conditions as could be achieved in a swim tunnel.

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